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## Research

### Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems

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Disturbance regimes are changing in forests across the world in response to global climate change. Despite the profound impacts of disturbances on ecosystem services and biodiversity, assessments of disturbances at the global scale remain scarce. Here, we analyzed natural disturbances in boreal and temperate forest ecosystems for the period 2001–2014, aiming to 1) quantify their within- and between-biome variation and 2) compare the climate sensitivity of disturbances across biomes. We studied 103 unmanaged forest landscapes with a total land area of  $28.2 \times 10^6$  ha, distributed across five continents. A consistent and comprehensive quantification of disturbances was derived by combining satellite-based disturbance maps with local expert knowledge of disturbance agents. We used Gaussian finite mixture models to identify clusters of landscapes with similar disturbance activity as indicated by the percent forest area disturbed as well as the size, edge density and perimeter–area-ratio of disturbed patches. The climate sensitivity of disturbances was analyzed using Bayesian generalized linear mixed effect models and a globally consistent climate dataset. Within-biome variation in natural disturbances was high in both boreal and temperate biomes, and disturbance patterns did not vary systematically with latitude or biome. The emergent clusters of disturbance activity in the boreal zone were similar to those in the temperate zone, but boreal landscapes were more likely to experience high disturbance activity

than their temperate counterparts. Across both biomes high disturbance activity was particularly associated with wildfire, and was consistently linked to years with warmer and drier than average conditions. Natural disturbances are a key driver of variability in boreal and temperate forest ecosystems, with high similarity in the disturbance patterns between both biomes. The universally high climate sensitivity of disturbances across boreal and temperate ecosystems indicates that future climate change could substantially increase disturbance activity.

Keywords: boreal forest, climate variability, disturbance regimes, remote sensing, spatial patterns, temperate forest

## Introduction

Disturbances shape vegetation structure, composition and distribution around the globe (Franklin et al. 2002, Virtanen et al. 2010, Ding et al. 2012). Agents such as fire, wind and insect outbreaks are key drivers of natural ecosystem dynamics (Turner 2010). Disturbance events happen abruptly, but can have lasting impacts on ecosystems (Yue et al. 2016, Thom et al. 2018). Especially in long-lived systems such as forests, disturbance-mediated alterations of the demographic structure of tree populations can prevail for decades to centuries (Schurman et al. 2018). Such disturbance-created patterns contribute to landscape heterogeneity (Burton et al. 2008), which – in combination with the species-rich early seral habitats resulting from natural disturbances (Swanson et al. 2011) – fosters biological diversity and determines ecosystem functioning (Mori et al. 2018).

Growing evidence suggests that the natural disturbance regimes of the world's forests are changing in response to climate change (Pureswaran et al. 2015, Trumbore et al. 2015, Seidl et al. 2017). In many parts of the world, such as in North America and Europe, disturbance activity has already increased strongly over the past decades (Seidl et al. 2014, Westerling 2016). Further increases in disturbance frequency and severity are expected for the coming decades as climate continues to change (Seidl et al. 2009, Wotton et al. 2010, Moritz et al. 2012).

These ongoing changes in natural disturbance regimes are of concern for policy makers and ecosystem managers because disturbances have a predominately negative impact on ecosystem service supply (Thom and Seidl 2016, Boucher et al. 2018). Increasing natural disturbances can, for instance, counteract policies aiming to mitigate climate change via increased carbon storage in forests (Kurz et al. 2008). Moreover, changes in forest disturbance regimes could fundamentally alter the organization and assemblage of the earth's vegetation. Biomes are primarily differentiated via dominant vegetation types, which, in turn, can strongly be modified by the prevailing disturbance regime (Mucina 2019). Wildfire – vegetation feedbacks are, for instance, important determinants of grassland – forest ecotones around the globe (Hoffmann et al. 2012, Cowling and Potts 2015). Climatically altered disturbance regimes could thus tip the scales between adjacent biomes and facilitate major changes in the global distribution of vegetation (Gauthier et al. 2015).

Due to their fundamental importance for ecosystem structure and functioning, disturbances have also come into the

focus of the global vegetation modeling community. The development of dynamic global vegetation models (DGVMs) has progressed greatly in recent years (Fisher et al. 2018), and increased consideration of tree demography in these models now allows them to simulate disturbances (Kautz et al. 2018). However, global reference data sets to benchmark the disturbance regimes emerging from such simulations remain largely missing to date. Furthermore, whether the disturbance–climate relationships used in large-scale models are consistent across biomes remains unclear.

Hampering a quantitative understanding of global forest disturbance regimes is the fact that disturbances are defined, measured and analyzed differently in different ecosystems around the globe. Despite a long-standing plea for generalization in disturbance ecology (White and Jentsch 2001) and a growing body of research on forest disturbances, the ability to directly compare between local studies remains limited. The proliferation of remote sensing approaches for assessing forest disturbances (Kennedy et al. 2014, Senf et al. 2017) offers great potential in this regard, as satellite-based remote sensing products provide a disturbance quantification that is consistent across the globe. Consequently, the first large-scale analyses of forest disturbances have emerged in recent years. Yet, these analyses have largely focused on within-biome variation in disturbances (Cohen et al. 2016, Senf et al. 2018, Sommerfeld et al. 2018, Kulha et al. 2019), or focused on a single disturbance agent (Kautz et al. 2017, Marini et al. 2017), while investigations across biomes covering the entire disturbance regime remain scarce.

A key limitation for the application of current remote sensing approaches in the context of disturbance ecology remains their inability to distinguish between different agents of forest disturbance. At the global scale, human land-use is a key disturbance agent of forest canopies (Curtis et al. 2018). Distinguishing changes in natural ecosystem dynamics from changes in human land-use thus remains a key challenge when working with remotely sensed disturbance data. Protected areas and areas of minimal human intervention offer important insights in this regard, serving as reference sites for the analysis of patterns emerging from natural processes. We here build on a previously established global network of unmanaged forest landscapes for the temperate zone (Sommerfeld et al. 2018). In this contribution we extend this network by more than doubling the number of landscapes and almost tripling the area covered by these landscapes in order to – for the first time – quantify inter- and intra-biome

differences in recent natural disturbances of boreal and temperate forests.

Our main objective was to compare recent natural disturbances in forest ecosystems between the boreal and temperate biomes. Specifically, we asked whether 1) between-biome differences in disturbance activity (jointly described here by four indicators, namely the percent forest area disturbed as well as the size, edge density and perimeter–area-ratio of disturbed patches) are greater than within-biome differences. Biomes are primarily identified via differences in dominant vegetation, and the associated differences in tree traits confer differences on the susceptibility of forests to natural disturbances (e.g. varying flammability of broadleaved-dominated and conifer-dominated forests). However, also disturbance–vegetation feedbacks are important drivers of abrupt vegetation changes at biome boundaries (Hoffmann et al. 2012, Moncrieff et al. 2015, Dantas et al. 2016). We thus expected distinctly different disturbance patterns between the temperate and boreal biome. Furthermore, we asked whether 2) disturbance regimes in the boreal biome differ from their counterparts in the temperate biome with regard to their climate sensitivity (i.e. the response of disturbance activity to variation in climate). Climate sensitivity is strongly driven by the prevailing disturbance agent and the underlying mechanisms determining disturbance activity (e.g. fuel moisture in the context of fire (Flannigan et al. 2016) and climate-mediated insect population dynamics in the context of insect outbreaks (White 2015)). As wildfire and insect outbreaks are the main agents of disturbance across boreal and temperate forests we tested the hypothesis that disturbances respond similarly to variation in temperature and precipitation. Specifically, we expected that warmer and drier than average conditions will facilitate disturbance activity throughout the boreal and temperate biome (Seidl et al. 2017).

## Material and methods

### A network of unmanaged forest landscapes

To address the inter- and intra-biome disturbance variation in forests of the boreal and temperate zone we here extended a previously compiled dataset of 50 temperate forest landscapes (Sommerfeld et al. 2018) to the boreal biome. We generally followed the biome delineation suggested by Olson et al. (2001), who combined a number of major previous biogeographic maps, integrating information from more than 1000 biogeographers, taxonomists, conservation biologists and ecologists from around the world. We compiled information for 53 unmanaged landscapes in seven countries spanning the circumpolar boreal forest biome, covering an area of  $20.3 \times 10^6$  ha (median landscape size: 57 714 ha). Criteria for landscape selection were 1) a contiguous polygon of at least 2000 ha that 2) has not been influenced by management during the study period 2001–2014 (Sommerfeld et al. 2018). Landscapes thus include core zones of protected areas (e.g. cat.

I or II according to the International Union for Conservation of Nature) as well as natural areas without formal protection status that have not been influenced by management interventions (based on the assessment of local experts). For each of the study landscapes we combined remotely sensed disturbance information (see next section) with field-based ecological knowledge from local experts. Specifically, information on dominant disturbance agents was collected from experts via a questionnaire, ranking them in decreasing order of importance (Supplementary material Appendix 1). Experts were identified via their publication record on the topic of forest disturbances for the selected areas, and all consulted experts also contributed to the analysis and interpretation of the data (Supplementary material Appendix 2).

Overall, the combined dataset of temperate and boreal landscapes analyzed here consisted of 103 landscapes with a total area of  $28.2 \times 10^6$  ha, covering a wide climatic gradient with mean annual temperatures ranging from  $-15.1^\circ\text{C}$  to  $14.8^\circ\text{C}$  and annual precipitation sums between 289 mm and 2315 mm. The dataset spans a latitudinal gradient from  $35.73^\circ\text{N}$  to  $70.55^\circ\text{N}$  and from  $36.20^\circ\text{S}$  to  $51.04^\circ\text{S}$ , and contains landscapes from five continents and both the northern ( $n = 81$ ) and southern ( $n = 22$ ) hemispheres (Fig. 1).

### Disturbance data and landscape pattern analyses

We retrieved global forest cover change maps from Hansen et al. (2013) for the period 2001–2014 (updated ver. 1.2). They mapped forest canopy change at a 30 m resolution consistently across the globe based on Landsat satellite data. Only areas stocked with trees  $> 5$  m height are considered forest, and only high severity disturbances (i.e. events where a disturbance leads to a complete or near complete removal of canopy trees at the level of a 30 m pixel) are mapped. Pixels are analyzed for disturbances independently of their neighboring pixels, and only the first disturbance of a pixel during the study period is considered. The dataset includes forest cover changes regardless of the agent causing the disturbance (Curtis et al. 2018). By studying unmanaged landscapes we here focused on natural disturbances.

The global forest cover change map was cropped to each study landscape, and four metrics of recent disturbance activity were calculated, using an eight-neighbor rule for defining adjacency between pixels, and considering all disturbances throughout the period 2001–2014. Metrics were selected to capture the extent and spatial patterns of disturbances, and pertain to two different spatial scales: at the landscape scale, we derived 1) the percent of the forest area disturbed (calculated as the total number of pixels disturbed relative to all forested pixels, and indicating the level of recent disturbance activity) and 2) the edge density of all disturbed patches within the forest area of a landscape (calculated by summing the length of all edges of disturbance-created patches and relating it to the total forest area, indicating the level of fragmentation of closed forest canopies caused by recent disturbances). At the scale of disturbed patches within a landscape we calculated



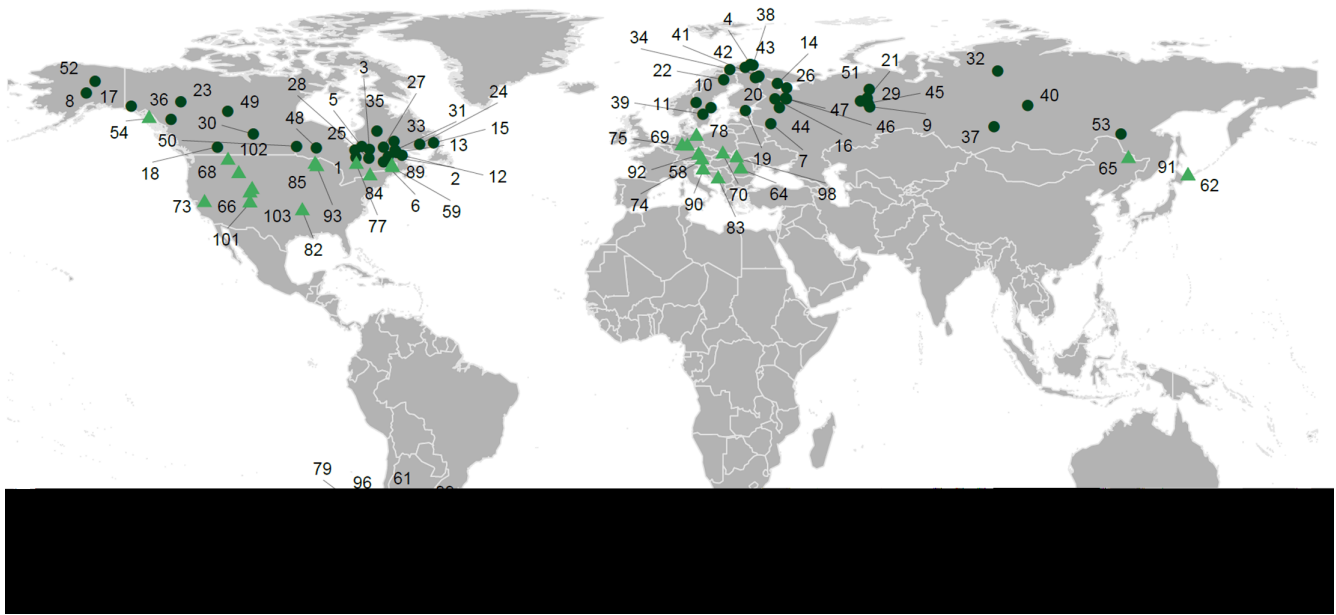


Figure 1. Global distribution of the 103 study landscapes. Biomes were generally delineated based on Olson et al. (2001) and further amended by assessments of local experts. See Supplementary material Appendix 2 for details on each landscape.

3) the area-weighted mean patch size (derived as the mean size of disturbed patches weighted by their size, and indicating the average extent of a disturbance-created patch) and 4) the area-weighted mean perimeter–area-ratio of disturbed patches (calculated as the ratio between patch edge length and patch size weighted by patch size, and describing the spatial complexity of patches). We used area-weighted patch metrics rather than arithmetic mean values across patches because the distribution of disturbance patches is highly skewed and area-weighted indices better represent the expected value that would be encountered when randomly sampling points on the landscape (Turner and Gardner 2015). The metrics calculated here are identical to those used in Sommerfeld et al. (2018) to characterize variation in natural disturbances within the temperate forest biome.

We analyzed the four disturbance metrics across absolute latitude using ordinary least squares regression, testing for broad biogeographical trends. Subsequently, we used unsupervised clustering via Gaussian finite mixture models (Fraley and Raftery 2007) to identify clusters of landscapes characterized by similar disturbance activity based on the four disturbance metrics described above. The number of clusters most strongly supported by the data was identified via the Bayesian information criterion (BIC). To address our first research question (between- versus within-biome variation) we compared the clusters of disturbance activity identified for the boreal biome to those previously described for the temperate biome (Sommerfeld et al. 2018). Comparisons included analyses at the level of the four disturbance metrics, as well as analyses in climate space (here defined by mean annual temperature and mean annual precipitation for the period 1960–1990, acquired from the WorldClim database ver. 1.4).

### Climate-sensitivity of disturbances

In order to investigate the climate sensitivity of disturbances (research question two) we used Bayesian generalized linear mixed effect models (GLMM), relating the annual area disturbed in each landscape to temperature anomaly, precipitation anomaly and their interaction. Climate anomalies were expressed as z-scores by subtracting the mean and dividing by the standard deviation from each annual value for 2001–2014. As the annual area disturbed is often highly skewed (and models are thus likely to be over-dispersed), and as disturbance data are frequently characterized by excessive zeros (i.e. years without disturbance), we used a negative binomial error distribution with a log link-function. Climate information was acquired from global NCEP/NCAR Reanalysis 1 data via the RNCEP interface (Kemp et al. 2012). We fitted one GLMM per disturbance activity cluster (identified via the unsupervised clustering described above) and biome, with random intercepts and slopes among landscapes. Our model structure thus accounted for the widely varying landscape sizes within each biome–cluster combination. Joint posterior distributions for all model parameters (temperature anomaly, precipitation anomaly, their interaction and the dispersion parameter of the negative binomial model) were fitted using Monte-Carlo Markov Chain methods implemented in Stan (Carpenter et al. 2017). We put mildly regularizing  $N(0, 10)$  priors on the intercept and slope parameters (temperature anomaly, precipitation anomaly and their interaction), reducing the risk of over-fitting. For the dispersion parameter we used a weakly-informative  $\text{Exp}(1)$  prior, and for the variance–covariance matrix of the random intercept and slopes we used a regularizing LKJ(1) prior. As temperature and precipitation might have lagged effects on disturbance activity, we considered different lags from one to three years in relating temperature and precipitation anomalies









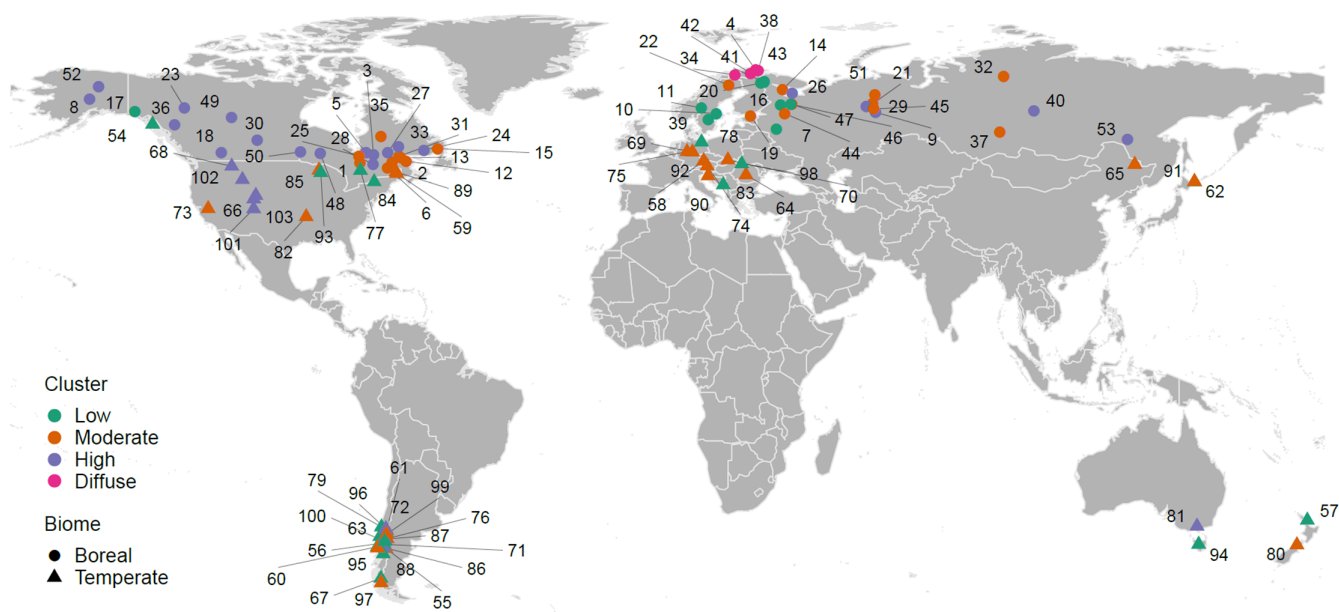


Figure 4. Global distribution of the four clusters of disturbance activity identified. For landscape IDs and meta-information on each landscape see Supplementary material Appendix 2.

Climate sensitivity between biomes was similar for landscapes with high disturbance activity, underlining that large fire events are consistently linked to warm and dry climatic conditions. A further factor contributing to similarities between biomes in areas with large disturbance activity could be that large disturbance events are increasingly decoupled from climate once they exceed a given size (e.g. with fire creating its own fire weather, and insect disturbances being decoupled from climate when population densities are high (Peters et al. 2004, Raffa et al. 2008)).

Assessing inter- and intra-biome variation in ecological patterns provides a quantitative baseline for the assessment of future changes in disturbances in response to climate change. Such baselines are particularly important for natural disturbances, as disturbance regimes are highly variable and any attempt to detect changes needs to distinguish them from the inherent variability of the system (Mori 2011). Here we for the first time quantified natural disturbance patterns across a wide range of boreal and temperate forests, highlighting that

tremendous within-biome variability is indeed a key characteristic of natural disturbance regimes across the globe. This variability in space and time results in a wide variety of structural patterns in forest ecosystems, and thus fosters their biological diversity (Burton et al. 2008, Mori et al. 2018).

Disturbances are important drivers of vegetation dynamics at biome boundaries in tropical ecosystems, with disturbance–vegetation feedbacks contributing to the formation of alternative biome states (Hoffmann et al. 2012, Moncrieff et al. 2015, Dantas et al. 2016). We here tested the hypothesis that disturbances are also an important factor differentiating temperate and boreal forests, expecting distinctly different disturbance regimes in the two biomes. Our data did not support this hypothesis, with disturbance patterns varying little across latitude, and similar disturbance activity groups emerging for both biomes in an unsupervised cluster analysis. Specifically, areas of high disturbance activity in the temperate zone had similar disturbance characteristics as such areas in the boreal zone. Furthermore, also in the boreal zone a sizeable share

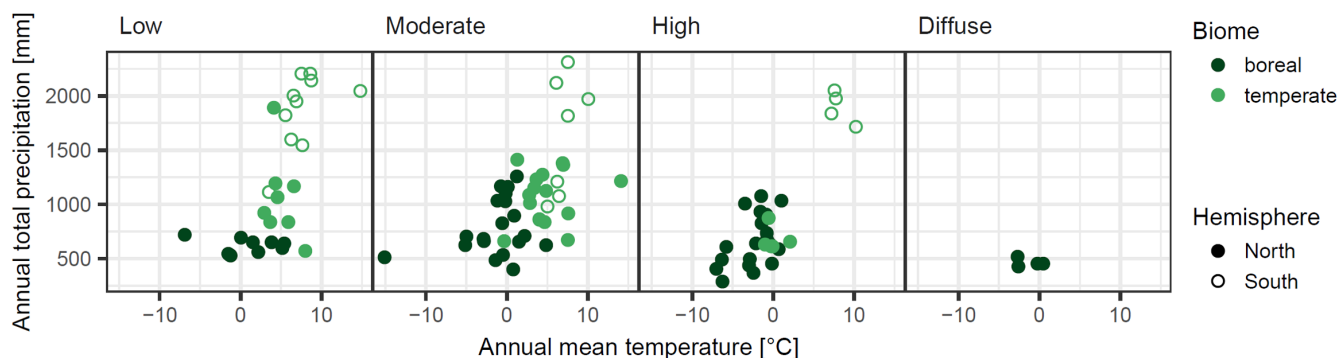


Figure 5. Location of the study landscapes in climate space for the four global clusters of disturbance activity.

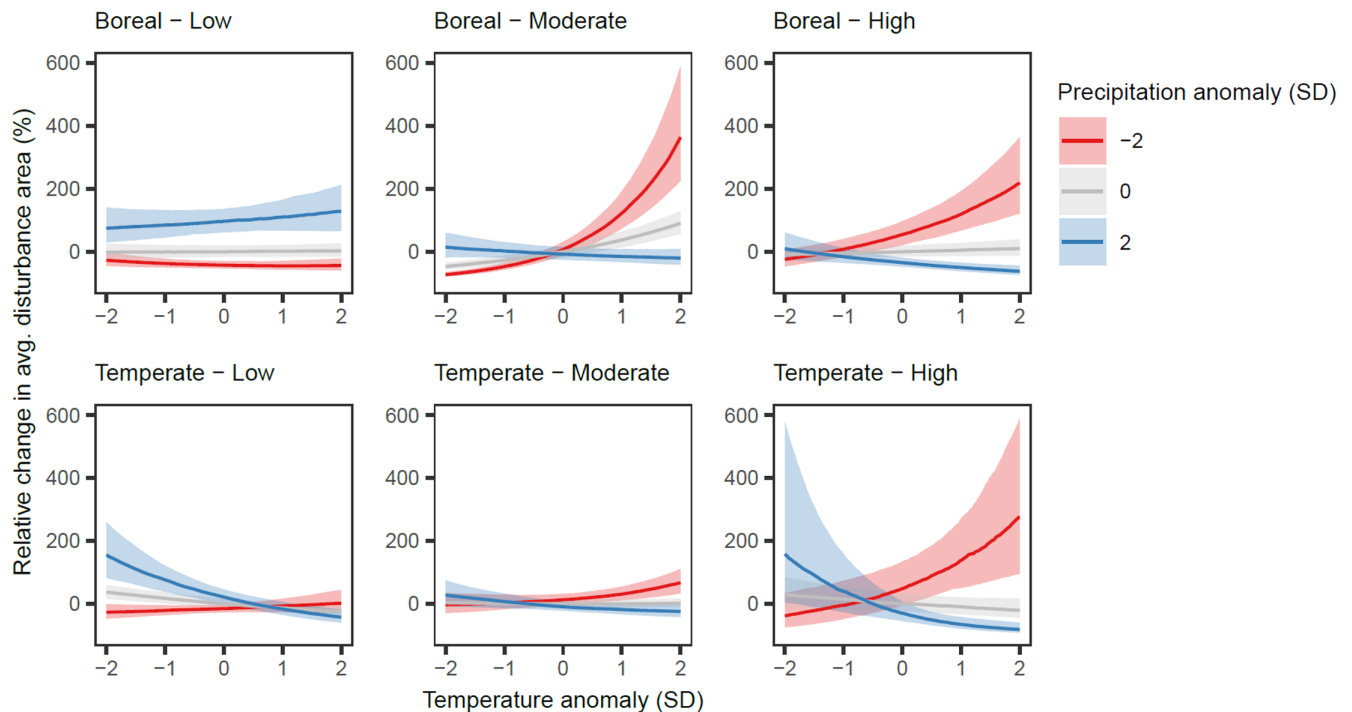


Figure 6. Predicted change of disturbed area relative to the mean in response to variation in temperature and precipitation for two biomes (rows) and three disturbance activity clusters (columns). Anomalies for temperature (x-axis) and precipitation (colors) are expressed in units of standard deviation (SD), with a value of zero indicating average conditions.

of landscapes experienced only very low disturbance activity during the 14-yr study period. While disturbance activity clusters were similar in the boreal and temperate zone, their prevalence differed between biomes, with boreal landscapes being more frequently associated with high disturbance activity than their temperate counterparts.

### Limitations

An important limitation of our approach lies in the nature of the remotely sensed data used here (Hansen et al. 2013). First, our study period (2001–2014) is comparatively short for studying rare events such as natural disturbances. We aimed to address the resultant stochasticity by studying disturbances across a large spatial extent, compiling a set of forest landscapes distributed throughout the globe. Nonetheless, future work should further scrutinize our findings, e.g. by making use of the full length of the Landsat observation period (at least from 1984 onwards), which would more than double the temporal scope of the analysis (Cohen et al. 2016, Senf et al. 2018). A further limitation related to our data arises from the fact that the forest definition applied here only identifies vegetation canopies of > 5 m in height as forests (Hansen et al. 2013). Particularly in the northern boreal biome this threshold means that many ecosystems that would still be characterized as forests in the field are outside of the scope of our remote sensing-based analysis (Guindon et al. 2018). More work on the disturbance regimes of the circumpolar northern boreal forest is thus needed to better contextualize our

findings regarding the diffuse disturbance activity cluster. A third limitation is the focus on stand-replacing (at the grain of a 30×30 m pixel) disturbances, which is not able to fully account for the complexities of natural disturbance regimes in forest ecosystems, e.g. with regard to stands only partially affected by disturbance. Systems with low- to moderate-severity and/or mixed-severity disturbance are prevalent around the globe (Perry et al. 2011, Meigs et al. 2017). The resultant live tree legacies play an important role for the recovery from disturbances (Jõgiste et al. 2017), yet they cannot be satisfactorily described with the data used here. Moreover, due to limitations in detection, some disturbance types (e.g. insect defoliation) might be underrepresented in the dataset analyzed here. Also, metrics such as the perimeter–area-ratio can be biased in coarse raster data (Bogaert et al. 2000). Finally, it is important to note that despite our relatively large sample the variability of natural disturbances in the boreal and temperate biome might not be fully captured in our data. Unmanaged landscapes in the temperate zone are frequently also smaller than their counterparts in the boreal zone, which could induce a bias in our inter-biome comparison. The resultant undersampling of rare, large events in the temperate zone does, however, further support our finding of large disturbances being prevalent in both biomes (cf. Table 1).

### Implications

Our results underline that natural disturbances are strongly climate-sensitive processes. Specifically, we highlight that

forest disturbances are likely to increase under warmer and drier conditions in boreal and temperate forests (Seidl et al. 2017). This finding of high climate sensitivity underlines the need for robust projections of future disturbance regimes in order to gauge their impacts on ecosystems and the services they provide to society (Scheller et al. 2018, Seidl et al. 2019). In this context our finding of consistent climate sensitivity of disturbances across biomes has important implications for ongoing efforts to improve disturbance modeling in DGVMs (Chen et al. 2018, Kautz et al. 2018), indicating that well-parameterized models might be applicable not only within biomes but also across biome boundaries. Furthermore, our finding of high inter-biome variability can serve as an important benchmark for pattern-oriented modeling of disturbance (Grimm and Railsback 2012).

A key element explaining intra-biome differences in disturbance activity are the prevailing disturbance agents. This underlines the importance of determining locally important disturbance agents to understand (and subsequently predict) disturbance regimes. It also suggests that the introduction of new disturbance agents (e.g. invasive alien pests (Hudgins et al. 2017)) can have a considerable impact on the disturbance regime (and its climate sensitivity). While distinguishing between human and natural causes of canopy disturbances is already possible via remote sensing (Guindon et al. 2014, Curtis et al. 2018), resolving different natural disturbance agents remains challenging. Here, we successfully combined local expert knowledge with large-scale remote sensing products, which can increase the inferential potential of remote sensing data for ecological questions. In conclusion, our analysis highlights remarkable similarities in disturbance patterns across boreal and temperate forest ecosystems (e.g. with regard to their spatial patterns and climate sensitivity), yet also underlines the considerable variation inherent to natural disturbances. While this variation is a challenge for assessing and predicting disturbance change, it is an important factor contributing to the diverse nature of forest ecosystems.

### Data availability statement

Data on forest disturbances were derived from the global forest change data set (Hansen et al. 2013) available at <<https://earthenginepartners.appspot.com/science-2013-global-forest>>. Data on temperate forest landscapes were taken from Sommerfeld et al. (2018) and are published in full in their Supporting information. Data on boreal forest landscapes were derived by means of a questionnaire (Supplementary material Appendix 1), and is published in full in Supplementary material Appendix 2.

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*Author contributions* – RS and CS designed the study. All authors contributed data. CS and JH conducted the analyses. RS wrote the text with contributions from all authors.

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Supplementary material (available online as Appendix ecog-04995 at <[www.ecography.org/appendix/ecog-04995](http://www.ecography.org/appendix/ecog-04995)>). Appendix 1–3.